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Productivity overshadows temperature in determining soil and ecosystem respiration across European forests

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Abstract

This paper presents CO_2 flux data from 18 forest ecosystems, studied in the European Union funded EUROFLUX project. Overall, mean annual gross primary productivity (GPP, the total amount of carbon (C) fixed during photosynthesis) of these forests was $1380 \pm 330\,\mathrm{gC\,m^{-2}\,y^{-1}}$ (mean ± SD). On average, 80% of GPP was respired by autotrophs and heterotrophs and released back into the atmosphere (total ecosystem respiration, $\mathrm{TER} = 1100 \pm 260\,\mathrm{gC\,m^{-2}\,y^{-1}}$). Mean annual soil respiration (SR) was $760 \pm 340\,\mathrm{gC\,m^{-2}\,y^{-1}}$ (55% of GPP and 69% of TER).

Among the investigated forests, large differences were observed in annual SR and TER that were not correlated with mean annual temperature. However, a significant correlation was observed between annual SR and TER and GPP among the relatively undisturbed forests. On the assumption that (i) root respiration is constrained by the allocation of photosynthates to the roots, which is coupled to productivity, and that (ii) the largest fraction of heterotrophic soil respiration originates from decomposition of young organic matter (leaves, fine roots), whose availability also depends on primary productivity, it is hypothesized that differences in SR among forests are likely to depend more on productivity than on temperature.

At sites where soil disturbance has occurred (e.g. ploughing, drainage), soil espiration was a larger component of the ecosystem C budget and deviated from

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the relationship between annual SR (and TER) and GPP observed among the less-disturbed forests. At one particular forest, carbon losses from the soil were so large, that in some years the site became a net source of carbon to the atmosphere. Excluding the disturbed sites from the present analysis reduced mean SR to $660 \pm 290\,\mathrm{gC\,m^{-2}\,y^{-1}}$, representing 49% of GPP and 63% of TER in the relatively undisturbed forest ecosystems.

Keywords: disturbance, eddy covariance, EUROFLUX, productivity, soil respiration, temperature, total ecosystem respiration

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Introduction

Soils and soil respiration are of particular importance in the global carbon (C) cycle (Houghton *et al.* 1995; Schimel 1995). Because soil organic matter (SOM) contains twice the amount of C stored in the atmosphere (Post *et al.* 1982), small changes in the soil C pool could strongly affect atmospheric CO_2 concentrations (Jenkinson 1991). While soils are currently assumed to be C sinks (Scholes 1999), accelerated rates of SOM decomposition in response to global warming may turn them into sources, resulting in a positive feedback to global warming (Schleser 1982; Jenkinson 1991; Raich & Schlesinger 1992; Smith *et al.* 1997; Scholes 1999; but see discussions by Townsend *et al.* 1992; Giardina & Ryan, 2000).

This hypothesized transfer of C from soils to the atmosphere in response to climatic warming is based mainly on the excellent global reviews showing soil respiration to increase in warmer climates (Fung *et al.* 1987; Raich & Schlesinger 1992; Raich & Potter 1995) and on the assumption that decomposition will accelerate faster than productivity in response to global warming (Kirschbaum 1995). However, in a recent study on the total amount of C present in similar soils in boreal coniferous forests, it was shown that soil C storage did not decrease, but increased with temperature in both high and low productive forests (Liski & Westman 1997; Liski *et al.* 1999). The authors concluded that the positive effect of higher temperatures on soil C inputs was far more important than the effect on C losses through SOM decomposition. Furthermore, recent evidence indicates that decomposition of SOM in the mineral soil does not vary with mean annual temperature (Giardina & Ryan, 2000).

The results presented in this paper support the latter studies and contradict the presumption that temperature is the dominant predictor of soil respiration. It will be shown herein that, across a wide range of European forest ecosystems, annual soil and ecosystem respiration are not correlated with mean annual temperature; furthermore, it will be hypothesized that primary productivity and site disturbance history exert a larger influence on these processes.

Net C exchange between forest ecosystems and the atmosphere (net ecosystem exchange, NEE) is determined by the difference between gross photosynthetic uptake and respiratory losses of CO_2, and is typically an order of magnitude smaller than these nearly offsetting terms (Jarvis 1995; Goulden *et al.* 1996a). Total ecosystem respiration (TER) is a composite flux, comprising aboveground respiration by foliage and woody tissues, and belowground respiration by roots (autotrophic soil respiration) and by soil organisms (heterotrophic soil respiration). Soil respiration (SR) is generally the largest flux contributing to TER, but few studies have simultaneously measured TER and SR by independent methods in forests. Reported estimates of the relative contribution of soils to TER range between 50 and 80% (Lavigne *et al.* 1997; Davidson *et al.* 1998; Law *et al.* 1999), highlighting the importance of SR in forest ecosystem C budgets. In this paper, the importance of SR is confirmed and it is shown that soil disturbance may enhance the role of soils in forest ecosystem carbon budgets.

Materials and methods

Site description

Measurements of NEE and SR were made at the sites of the European EUROFLUX network (Valentini *et al.* 2000), which encompasses a large range in European climates and tree species (Table 1). More detailed descriptions of all sites included in this analysis can be found in Valentini (2001), and in the References cited in Table 1.

Soil respiration

No standardized method was defined for measuring soil CO_2 efflux and consequently about 14 different systems were used. All techniques are described in detail by Lankreijer *et al.* (2001). Soil chambers connected to infrared gas analysers (dynamic chamber systems) were most common, and this analysis only includes data

Table 1 Overview of the EUROFLUX forest ecosystems. Site codes used in the graphs*, location, elevation (m a.s.l.), dominant tree species** and mean stand age (y) are given. Temp, long-term mean annual air temperature (°C); Precip, long-term mean annual precipitation (mm). TER (total ecosystem respiration) and SR (soil respiration) columns indicate which data were available at each of the sites (* in SR column indicates data were rejected for methodological reasons)

Site	Site code	Location	Elevation	Species	Age	Period	Temp	Precip	TER	SR	References
Italy2	A	41°45′N 12°22′E	3	2	30	1997	15.3	770	–	*	(Dore 1999)
Italy1	B	41°52′N 13°38′E	1550	1	90	1996 – 97	7	1100	+	*	(Matteucci 1998)
France2	C	44°05′N 0°05′E	60	10	25	1996–97	13.5	900	+	–	(Hassika & Berbigier 1998)
Italy ex	D	46°35′N 11°26′E	1730	mix 4, 6	80	1998	4.1	1010	–	*	(Montagnani 1999)
France1	E1, E2, E3	48°40′N 7°05′E	300	1	30	1996, 1997, 1998	9.2	820	+	+	(Epron *et al.* 1999; Granier *et al.* 2000)
Germany1	Fa, Fb, Fc, Fd	50°09′N 11°52′E	780	4	48, 87, 111, 146	1997–98	5.8	890	+	+	(Buchmann, 2000; Valentini, 2001)
Belgium1	Ga1, Ga2, Gb	50°18′N 6°00′E	450	1, 1, 7	60–90	1997 1998, 1997	7	1000	+	+	(Longdoz *et al.* 2000)
Germany2	H1, H2, H3	50°58′N 13°38′E	380	mix 4, 11	99	1996 1997, 1998	7.5	820	+	–	(Valentini, 2001)
Belgium2	I	51°18′N 4°31′E	20	mix 5, 3	70	1997	10	750	–	*	(Kowalski *et al.* 1999)
Germany-ex	J1, J2	51°46′N 9°35′E	505	4	110	1996, 1997	6.6	1050	+	–	(Ibrom *et al.* 1996)
Netherlands	K	52°10′N 5°45′E	25	5	80	1997	10.3	770	+	–	(Valentini, 2001)
Germany-Kiel	L	54°06′N 10°14′E	49	1	100–105	1998	8.1	697	–	+	(Kutsch *et al.* 2001)
Danmark	M1, M2, M3	56°00′N 12°20′E	40	1	100	1996–97, 1997–98, 1998–99	8	600	+	+	(Pilegaard *et al.* 2000)
United Kingdom	N1, N2	56°37′N 3°48′E	340	8	14	1997, 1998	8	1400	+	–	(Valentini, 2001)
Sweden1	O1, O2, O3, O4	60°05′N 17°28′E	45	Mix 4, 5	80–100	1995 1996, 1997, 1998	5.5	530	+	+	(Lindroth *et al.* 1998; Morén & Lindroth, 2000)
Finland	P	61°51′N 24°17′E	170	5	35	1997	3.5	640	+	–	(Vesala *et al.* 1998)
Iceland	Q	63°50 N 20°13′W	78	9	5	1997	3.6	1120	+	–	(Valentini, 2001)
Sweden2	R	64°07′N 19°27′E	310	4	31	1997	1	570	+	–	(Valentini, 2001)

*Site codes should be interpreted as follows: capital letters indicate different sites (labelled A to R according to latitude), lower case letters refer to different species or age classes within the same site, which can be found in the ‘Species’ and ‘Age’ columns. Numbers following letters indicate different measurement years and are listed in the ‘Period’ column.

** Species: 1, *Fagus sylvatica*; 2, *Quercus ilex*; 3, *Quercus robur*; 4, *Picea abies*; 5, *Pinus sylvestris*; 6, *Pinus cembra*; 7, *Pseudotsuga menziesi*; 8, *Picea sitchensis*; 9, *Populus trichocarpa*; 10, *Pinus pinaster*; 11, *Larix decidua* obtained with such dynamic chamber systems. Furthermore, results were excluded that were obtained with one soil chamber (SRC-1, PP-Systems, UK), because recent intercomparison studies have suggested that this chamber system measures higher soil fluxes compared to other chamber systems (Le Dantec *et al.* 1999; Janssens *et al.* 2001).

Estimates of annual SR were obtained by extrapolation of regression functions relating measured soil CO_2 efflux to soil temperature (and moisture). At most sites, the empirical functions explained 80–90% of the temporal variability in SR (Epron *et al.* 1999; Janssens *et al.* 1999; Buchmann, 2000; Morén & Lindroth, 2000), while in the drought-stressed Mediterranean sites they explained only 60–70% of the variation (Dore 1999; Matteucci *et al.* 2000). A wide range of temperature and moisture response functions was applied among the different sites. Janssens *et al.* (2001) investigated the effect of different temperature and moisture response functions on the simulated soil fluxes and found that different regression functions resulted in very similar estimates of the total annual flux (< 1% difference), although predictions diverged under certain conditions within the year. Thus, the implementation of different regression functions probably did not add to variability in the estimation of annual SR among the sites.

Total ecosystem respiration and gross primary productivity

At the EUROFLUX sites, net ecosystem exchange (NEE) was measured by a standardized eddy covariance methodology, described in detail by Aubinet *et al.* (2000). Total ecosystem respiration (TER) was calculated either as the sum of (i) night-time fluxes and (ii) daytime respiration, or (iii) as 24-h NEE fluxes for leafless periods (i.e. for deciduous forests). Functional relationships between well-mixed night-time fluxes ($u^* > 0.2$–$0.4\,\mathrm{m\,s^{-1}}$) and temperature were established at each site. These temperature functions were used for gap filling and correcting potential advective CO_2 losses during stable night-time periods ($u^* < 0.2$–$0.4\,\mathrm{m\,s^{-1}}$), and were extrapolated to daytime in order to estimate daytime respiration (see below). As respiration and advective CO_2 losses are site-dependent processes, no standard protocol was defined. Most teams used exponential functions, whereas a few teams used a modified Arrhenius function (Lloyd & Taylor 1994). Air or soil temperature, or a combination of both, was used in the temperature functions, whichever resulted in the best fit. At sites with dry soils (e.g. France 1) the response of ecosystem respiration to soil water content was included in the regression function to improve the extrapolation, while at the Italy 1 site, different temperature functions were applied depending on soil moisture conditions. At the Germany 2 site, the temperature function was fitted separately to data from different soil moisture classes, allowing the parameters of the function to change with soil moisture conditions. At the Iceland site, the temperature function was fitted to data from different periods, allowing the parameters of the function to change throughout the year. Annual gross primary productivity (GPP) was estimated as the sum of TER and net C uptake by the ecosystem (GPP = TER – NEE).

Estimates of TER and GPP derived from night-time eddy covariance fluxes are associated with large uncertainties. First, daytime TER is likely to differ from night-time TER because of light-induced inhibition of leaf respiration (Brooks & Farquhar 1985; Villar *et al.* 1994). The extrapolation of night-time respiratory fluxes therefore may have resulted in an overestimation of daytime and annual TER. Because this overestimation depends on the contribution of leaf respiration to TER and on the degree of inhibition during daytime, both of which are unknown and highly variable throughout the year, also the degree of overestimation is unknown. Nonetheless, preliminary calculations suggest that the upper limit for the overestimation of TER resulting from daytime inhibition of leaf respiration is around 15%.

Secondly, TER and GPP may also have been underestimated. As turbulence at night is sporadic, other forms of transport (e.g. advection) may become more important. Because the eddy covariance technique only captures turbulent transport of CO_2, advective losses of CO_2 will result in underestimated night-time fluxes and thus also lower TER estimates. Intercomparison experiments of night-time eddy covariance fluxes and upscaled chamber estimates of TER have indicated that this underestimation may amount up to 30% of TER (Goulden *et al.* 1996b; Lavigne *et al.* 1997; Law *et al.* 1999), although not every site is equally prone to suffer advective losses. Furthermore, at most sites data obtained in conditions of low turbulence have been corrected as described above, mitigating the degree of overestimation to some extent.

Thirdly, there is uncertainty in the regression functions used for gap filling, for correcting low turbulence data and for simulating daytime respiration. Because eddy covariance data inherently are highly variable, especially during night-time, large confidence intervals are typically associated with the fitted regression functions (mean ± 5–15%). Furthermore, different regression functions may result in different TER estimates, contributing to the uncertainty surrounding TER and GPP estimates based on eddy covariance data. In addition, daytime temperatures are higher than the night-time temperatures to which the regression functions were fitted. Because it is at these higher temperatures that different regressions differ most, their estimates of daytime respiration are also likely to differ.

The reader should bear in mind this large uncertainty associated with the values of TER and GPP reported in this study. Nonetheless, they represent the best estimates available to date.

The model EUROFLUX forest

Twenty-four datasets including annual GPP, TER and NEE data from 16 forests were integrated to construct the model EUROFLUX forest (two sites reported only NEE and were not included in the analysis). Mean values of GPP, TER and NEE were obtained by averaging these fluxes over the entire dataset. Because only SR data obtained with dynamic chamber systems were included, estimates of annual SR were available for only 10 out of the 24 datasets. In order to derive the mean soil flux for the model EUROFLUX forest, soil fluxes in the less disturbed forests for which no estimate of annual SR was available were estimated by extrapolating the relationship between SR and GPP observed across sites for which separate estimates of SR were available. The relationship between SR and GPP in the less disturbed forests is given in (eqn 2) (see Results and Discussion section). Mean SR of the model EUROFLUX forest was then estimated by averaging the entire dataset. Aboveground respiration was calculated as the difference between TER and SR.

Results and discussion

With the exception of the drought-stressed Mediterranean forests, temperature was the dominant factor controlling the seasonal changes in soil respiration *within* most of the investigated forests (Epron *et al.* 1999; Janssens *et al.* 1999; Buchmann, 2000; Morén & Lindroth, 2000). In contrast, there was no significant relationship between annual SR and mean annual temperature *among* the different EUROFLUX forests (Fig. 1). Furthermore, at several sites, there were significant differences in SR among different vegetation covers within the same forest. For example, at the Belgium 1 and Belgium 2 sites, annual SR under broadleaved tree species was twice that under coniferous trees (Janssens *et al.* 1999; Longdoz *et al.* 2000), and at the Germany 1 site, SR differed among spruce stands of different ages (Buchmann, 2000). Such large variability observed in the absence of differences in temperature and precipitation clearly suggests that other factors are more important in determining SR.

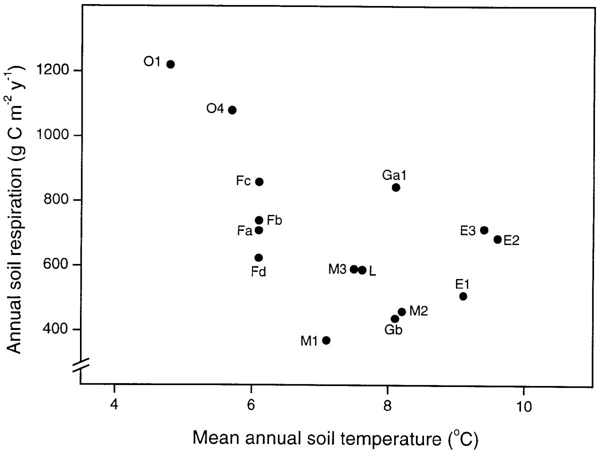

Fig. 1 Annual soil respiration vs. mean annual soil temperature. Site codes should be interpreted as follows: capital letters indicate different sites (listed in Table 1), lower case letters refer to different species or age classes within the same site (see 'Species' or 'Age' columns in Table 1), numbers following letters indicate different measurement years (listed in 'Period' column in Table 1).

As with SR, seasonal variability in TER *within* most of the forests was largely accounted for by variability in temperature (Lindroth *et al.* 1998; Granier *et al.* 2000). Again, however, there was no significant relationship between annual TER and mean annual temperature *among* the sites, not even when TER fluxes were analysed according to the year of measurement (Valentini *et al.* 2000). In 1996 and 1998, there was no correlation between TER and mean annual air temperature (Fig. 2), while the positive trend observed in 1997 was completely driven by the France 2 maritime pine plantation (C in Fig. 2).

That two independent estimates show temperature as a poor predictor of annual respiration clearly indicates that other factors are more important in controlling soil and ecosystem respiration between years and sites at regional and continental scales. Why does temperature exert such dominant control over temporal variability in respiration at a given site, yet does not explain differences in respiration among sites?

Soil respiration originates mainly from root (autotrophic) and microbial (heterotrophic) activity. At a given site, total root respiration will increase with temperature, because root biomass typically peaks in summer (Lyr & Hoffmann 1967) and because specific root respiration rates increase with temperature (Zogg *et al.* 1996). Thus, in the absence of drought stress, soil temperature will exert dominant control over autotrophic soil respiration. However, root respiration is coupled to shoot photosynthetic activity via a constant allometric allocation scheme in trees (Heilmeier *et al.* 1997). Because roots can only respire a proportion of what they are allocated, the effect of temperature on root respiration is likely to be

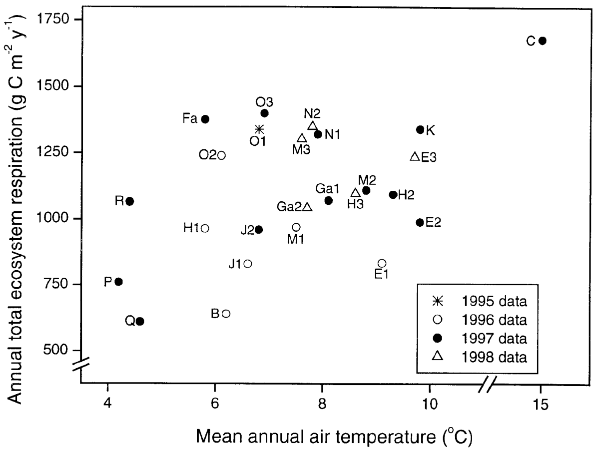

Fig. 2 Annual total ecosystem respiration vs. mean annual air temperature. Site codes should be interpreted as follows: capital letters indicate different sites (listed in Table 1), lower case letters refer to different species or age classes within the same site (see 'Species' or 'Age' columns in Table 1), numbers following letters indicate different measurement years (listed in 'Period' column in Table 1).

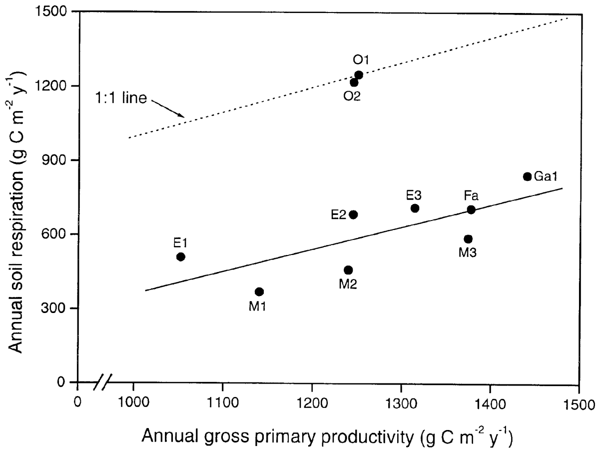

Fig. 3 Annual soil respiration vs. annual gross primary productivity. Site codes should be interpreted as follows: capital letters indicate different sites (listed in Table 1), lower case letters refer to different species or age classes within the same site (see 'Species' or 'Age' columns in Table 1), numbers following letters indicate different measurement years (listed in 'Period' column in Table 1). The dotted line represents the 1:1 line, the solid line gives the best linear fit for the less disturbed sites (see text for discussion).

constrained by GPP. Thus it seems likely that on an annual timescale GPP, more than temperature, can explain differences in autotrophic respiration among sites.

As with root respiration, soil temperature is likely to control soil heterotrophic activity at a given site (in the absence of drought stress). Heterotrophic respiration differs from autotrophic respiration in that there are large amounts of substrate waiting to be decomposed, suggesting that heterotrophic respiration rates might be independent from GPP. However, microbes preferably use the short-lived fractions of SOM as an energy source (Parton *et al.* 1987; Trumbore *et al.* 1990; Schimel *et al.* 1994) and therefore depend primarily on new litter inputs (Schulze *et al.* 2000), and thus, indirectly, also on site productivity (although a considerable time-lag may exist between carbon assimilation, leaf and root litter production and the actual decomposition).

This explains why temperature represents the main control over the temporal changes in soil respiration within sites, but variation amongst sites is likely to depend more on productivity and less on temperature. In support of this hypothesis, a positive correlation was observed between SR and GPP ($r = 0.76$, $n = 8$, $P = 0.0482$) among the EUROFLUX sites where soil disturbance was negligible (Fig. 3, see below for discussion). A similar dependence of SR on productivity was also shown for a grassland ecosystem (Craine *et al.* 1999).

The absence of a pronounced temperature dependence of SR *among* the EUROFLUX forests (Fig. 1) appears contradictory to reviews on global SR (Raich & Schlesinger 1992; Raich & Potter 1995), in which temperature is reported to be the single best predictor of SR in the absence of water-stress. However, within a mean annual temperature range comparable to that of our study (4–10 °C), these global reviews also showed very large variability that could not be explained by temperature alone. Thus, the present results are not as contradictory as one might expect at first sight. In addition, the above reviews also mentioned a positive correlation between SR and net primary productivity. Not only does this support the hypothesis suggested here, but it also implies that the observed increase of SR with temperature may result from an enhancement of productivity in warmer regions with faster nutrient cycling, higher irradiance and longer growing seasons. If the enhanced rates of SR at higher temperatures were solely the result of higher decomposition rates (Swift *et al.* 1979), soil C stocks would eventually decline, leading to decreasing SR rates with time. Higher rates of SR in warmer climates can thus be sustained only by higher productivity and subsequent root activity (respiration and exudation) and litter deposition (more substrates available for decomposition). Because productivity also depends on other factors, such as precipitation, soil fertility, vegetation cover, site history, the relationship between productivity and temperature is likely to be very weak over a small temperature range, and will appear only at larger scales. It is suggested that because

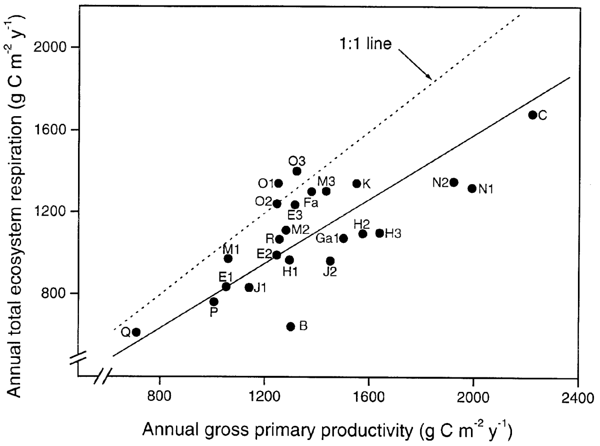

Fig. 4 Annual total ecosystem respiration vs. annual gross primary productivity. Site codes should be interpreted as follows: capital letters indicate different sites (listed in Table 1), lower case letters refer to different species or age classes within the same site (see 'Species' or 'Age' columns in Table 1), numbers following letters indicate different measurement years (listed in 'Period' column in Table 1). The dotted line represents the 1 : 1 line, the solid line gives the best linear fit (see text for discussion).

productivity determines SR, the weak correlation between productivity and temperature that was observed among the EUROFLUX sites explains why there was no correlation between soil respiration and temperature, although such a correlation does exist at the global scale (Raich & Schlesinger 1992).

In agreement with the SR data, a significant correlation between TER (R_t) and GPP (P_g) was observed among the EUROFLUX sites (eqn 1) although variability was considerable, especially among sites with moderate productivity (Fig. 4).

$$R_t = 0.79\,P_g\ (\mathrm{gC\,m^{-2}\,y^{-1}},\ P = 0.0002,\ R^2 = 0.53,\ n = 24) \qquad (1)$$

In a previous analysis of NEE in the EUROFLUX forests, Valentini and colleagues observed an increase in NEE (and in the TER/GPP ratio) with latitude across the non-intensively managed EUROFLUX sites (Valentini *et al.* 2000). This increase in the TER/GPP ratio with latitude across the non-intensively managed EUROFLUX sites may partly explain the high variability in the relationship between TER and GPP observed among the sites with moderate productivity (Fig. 4). In addition, as discussed below, site disturbance may explain the disproportionally high TER values in the Sweden 1 site (O1-O3 in Fig. 4), while the very low respiration rate in the Mediterranean beech site (B in Fig. 4) may be related to drought stress in summer, and snow and low temperatures in winter (Matteucci 1998; Valentini *et al.* 2000).

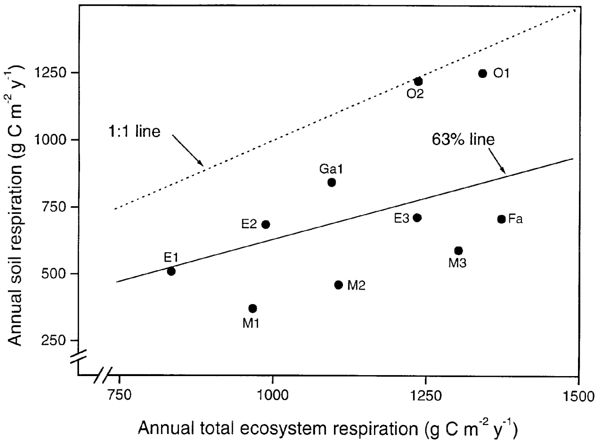

Fig. 5 Annual soil respiration vs. annual total ecosystem respiration. Site codes should be interpreted as follows: capital letters indicate different sites (listed in Table 1), lower case letters refer to different species or age classes within the same site (see 'Species' or 'Age' columns in Table 1), numbers following letters indicate different measurement years (listed in 'Period' column in Table 1). The dotted line represents the 1:1 line, the solid line represents the 63% line (the contribution of soil respiration to total ecosystem respiration in the EUROFLUX model ecosystem for slightly disturbed forests only).

Soil disturbance, e.g., may enhance the decomposition of chemically of physically protected SOM. In undisturbed soils, these older SOM pools contribute less to SR, and accelerating their decomposition will therefore confound the relationship between SR and productivity. The high TER rates in the young Sitka spruce site (N1 and N2 in Figs 2 and 4) can probably be attributed in part to enhanced decomposition and subsequent nitrogen release resulting from ploughing up what was a heathland/grassland site prior to afforestation. At the France 1 site, disturbance associated with thinning enhanced soil fluxes the following year (Epron, unpublished results). At the Sweden 1 site (O1–O3 in Figs 1–5), past drainage is likely to have enhanced soil aeration and to have increased heterotrophic respiration rates and accelerated decomposition of old SOM (Lindroth *et al.* 1998), resulting in the highest soil and ecosystem respiration rates among the EUROFLUX forests (Figs 1–4). Soil respiration equalled GPP (Fig. 3), and this particular site was the only EUROFLUX forest that was consistently losing C to the atmosphere in the late nineties (Lindroth *et al.* 1998; Valentini *et al.* 2000). Because disturbance only stimulates SR, its contribution to TER at this site was higher than at other sites (Fig. 5).

The model EUROFLUX forest annually sequestered 270 ± 230 $\mathrm{gC\,m^{-2}\,y^{-1}}$ (NEE) from the atmosphere into biomass or soil organic matter, indicating that the EUROFLUX forests are sequestering considerable

Table 2 CO_2 fluxes in the model EUROFLUX forest ecosystem (all sites = fluxes averaged over all datasets, $n = 24$) and in the model EUROFLUX ecosystem including only slightly disturbed forests (Sweden 1 and UK sites excluded, $n = 19$). GPP (annual gross primary productivity, TER (annual total ecosystem respiration) and NEE (annual net ecosystem exchange) were obtained by averaging the fluxes from the individual sites. For the estimates of SR (annual soil respiration) and AGR (annual above-ground respiration) the reader is referred to the Materials and methods section. SD indicates standard deviation

	EUROFLUX (all sites)		EUROFLUX (less disturbed sites only)	
CO_2 flux	Flux (SD) ($gC\,m^{-2}\,y^{-1}$)	Flux (% of GPP)	Flux (SD) ($gC\,m^{-2}\,y^{-1}$)	Flux (% of GPP)
GPP	1380 (330)	100	1340 (310)	100
NEE	−270 (230)	20	−290 (190)	22
TER	1100 (260)	80	1040 (260)	78
SR	760 (340)	55	660 (290)	49
AGR	340	25	380	29

amounts of C. On average, these forests annually fixed $1380 \pm 330\,gC\,m^{-2}\,y^{-1}$ through photosynthesis (Table 2) and respired the equivalent of 80% of this flux ($1100 \pm 260\,gC\,m^{-2}\,y^{-1}$). Soils exerted a central role in the C budget of the model EUROFLUX forest ecosystem, releasing $760 \pm 340\,gC\,m^{-2}\,y^{-1}$, the equivalent of 55% of GPP (Table 2). Soils contributed 69% to TER, which agrees well with other estimates found in the literature (Lavigne *et al.* 1997; Davidson *et al.* 1998; Schulze & Heimann 1998; Law *et al.* 1999). Interannual variability in these estimates was moderate: 3–11% for the contribution of soils to TER and 2–5% in the relation with GPP. In contrast, there are large differences among the different forests, even if the exceptional Sweden 1 site is ignored. For example, among the beech forests (sites E, M, Ga in Fig. 5), estimates of the relative contribution of soils to TER range between 38 and 79%. The use of different soil chambers may have contributed to this variability, but large differences were also found among sites where identical chambers were used (sites E, Fa, Ga in Fig. 5), thus indicating that the observed variability in the relative contribution of soils to TER is realistic.

Exclusion of the two sites with soil disturbance (sites N and O) from the model EUROFLUX forest reduces variability in the relative importance of SR in the carbon budget (Fig. 3). The relationship between SR (R_s) and GPP (P_g) in the less disturbed forests is expressed as:

$$R_s = -552 + 0.913\,P_g\ (gC\,m^{-2}\,y^{-1},\ P = 0.048,\ R^2 = 0.58,\ n = 8)\,. \tag{2}$$

This equation is highly empirical and is unlikely to apply at sites with very low or very high GPP. In the less disturbed model EUROFLUX forest, soils released less C: $660 \pm 290\,gC\,m^{-2}\,y^{-1}$, representing only 49% of GPP and 63% of TER (Table 2). However, as disturbance is common in European forests, it is likely that the true importance of SR in forest C budgets is closer to the overall average cited above (i.e. 55% of GPP).

Conclusions

Temperature exerted dominant control over seasonal variability in both SR and TER within the non water-stressed forests. Among the different forests, however, neither annual SR nor TER were found to be related to mean annual temperature. By contrast, SR and TER were significantly related to GPP among sites with limited soil disturbance.

It was hypothesized that SR is related to site productivity, which depends not only on temperature, but more importantly on other factors such as soil fertility, site history and vegetation cover. However, in one forest, soil drainage has apparently stimulated decomposition such that SR almost equalled GPP, turning the forest into a source of C to the atmosphere in some years, and confounding the relationship between annual SR and GPP that was observed among the less-disturbed forests.

In the model EUROFLUX forest, GPP was $1380 \pm 330\,gC\,m^{-2}\,y^{-1}$. Soils respired the equivalent of 55% ($760 \pm 340\,gC\,m^{-2}\,y^{-1}$) of GPP and contributed 69% of TER (TER = $1100 \pm 260\,gC\,m^{-2}\,y^{-1}$). When considering only slightly disturbed sites, the importance of soils for the forest ecosystem carbon budget decreased, with soils releasing 49% of GPP and contributing 63% of TER.

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